PEARL

The Journal of HEREDITY

THE MORLOK QUADRUPLETS CELEBRATE THEIR FIFTH BIRTHDAY
(SEE PAGE 147)

Genetics of Mouse Leukemia

A Genetic History of Brown Swiss Cattle

Chromosome Models Visualize Rival Theories

International Committee to Act on Congress Date

VOLUME 28 APRIL, 1937 NUMBER 4

The American Genetic Association

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The

Journal of Heredity

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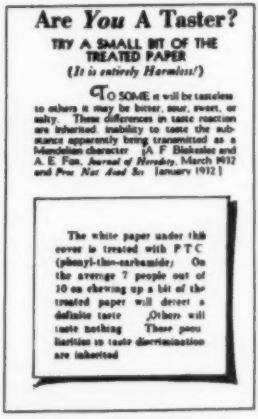
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LEAFLETS TO DEMONSTRATE HEREDITY

Last year the "Taster test" served as an introduction to human genetic differences in many classrooms. The test is so easily made with the treated paper, and arouses such great interest that it appears to have a definite place in group demonstrations of such differences. These leaflets, size 3⅜" by 5½", are available in quantities for those who wish to use them for classroom or lecture purposes. On the back is printed an outline 4-generation pedigree chart. Sample on request. Prices: 10 for 25c; 50 for $1.00.

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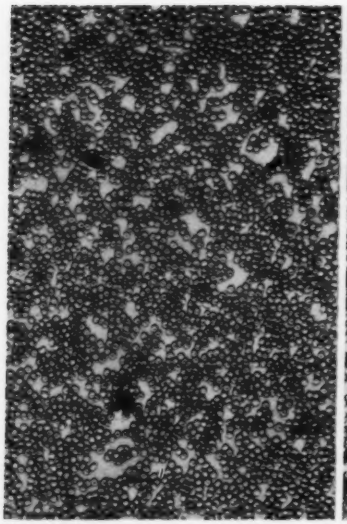
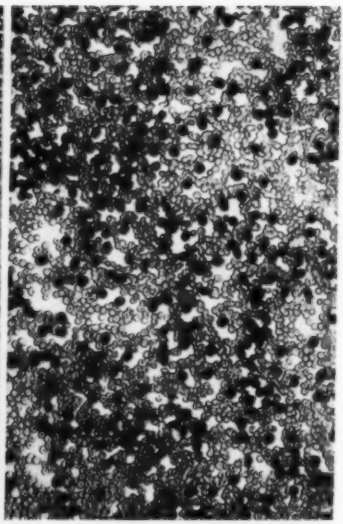


Normal Blood



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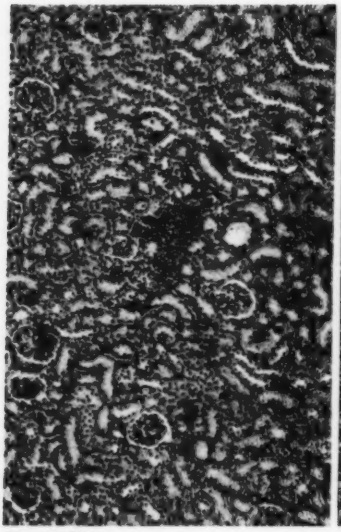
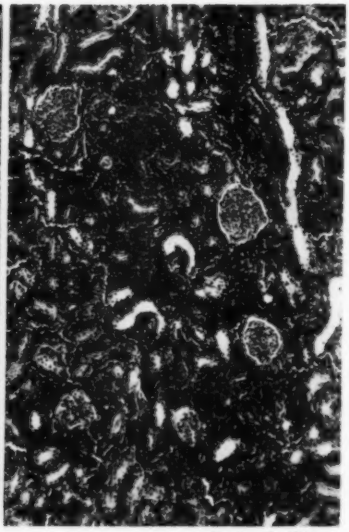


Normal Kidney



Leukemic Kidney

NORMAL AND LEUKEMIC TISSUES

Frontispiece

Leukemia is due to the uncontrolled growth of white blood cells. (These appear *black* in the above photographs because they have been made dark by Wright's stain so that they may be readily visible.) White blood cells play a very important part in the economy of warm-blooded animals, but their uncontrolled growth is a disease which is usually fatal to the organism. The two lower views show how the excess white blood cells are crowded into affected organs,—the kidney in this case. The great concentration of white blood cells has forced apart the tubules of the kidney, resulting in an enlargment of that organ. On the basis of transplantation studies leukemia is now recognized as a form of cancer affecting the blood (which is a mobile tissue) in the same way that cancerous loss of growth control affects lung, breast, and other tissues.

GENETICS OF MOUSE LEUKEMIA

E. C. MacDowell

Department of Genetics, Carnegie Institution of Washington, Cold Spring Harbor, Long Island, N. Y.

Leukemia is a tumorous disease in which the malignant growth is limited to white blood cells. These wild cells, constantly multiplying, may enter any or all organs and parts of the body; they often cause excessive enlargement of spleen and lymph nodes and enormously increase the number in the blood. The disease in its various manifestations is virtually identical in mouse and man. The only known method of direct transmission from a spontaneous case is by transplantation of living leukemic cells into a susceptible animal.

The following talk was presented in the Cancer Symposium of the Section on Medical Sciences of the American Association for the Advancement of Science at Atlantic City, December, 1936.—EDITOR.

YOU may have had the good fortune, any one of you, to inherit a house from your father. His house would have become your house.

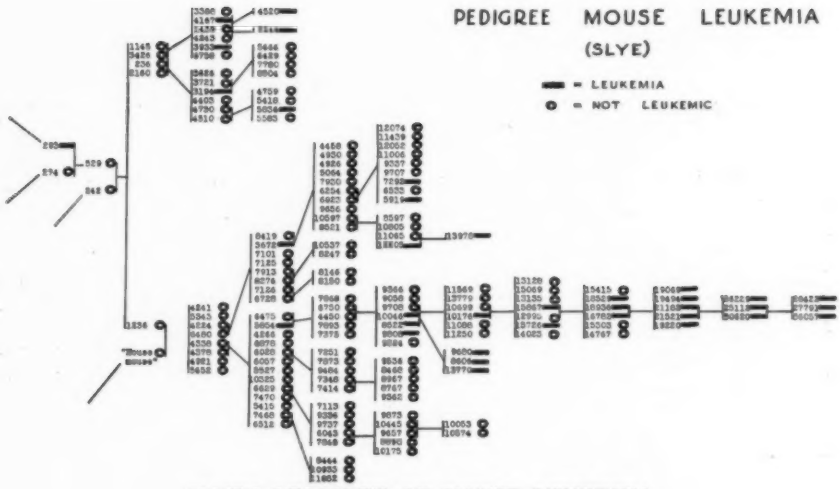
But if you had the misfortune to inherit leukemia, it would not have been your father's leukemia handed on to you, for your biological inheritance was transmitted some twenty years before your father's hypothetical leukemia appeared. You could not have inherited his leukemia as such, nor any other of his traits as such. You received only certain potentialities—which I shall call for short, potencies—and these potencies interacted with their surroundings in every step of your development from a fertilized egg to the present. These potencies are chemical substances that, like all other chemical substances, react differently according to the conditions encountered. Thus all your traits are the result of the cooperation between inherited potencies and their environments. This is true for any one of you; it is true for all of you. It is true for all animals and all plants. Life itself is an interaction between intrinsic and extrinsic influences.

Thus, a son resembles his father to the extent that similar potencies react with similar environments. These environments are largely controlled by the automatic processes of embryonic development, so that similar potencies frequently give similar results. This led the earlier students of heredity to talk as though receiving potency were the same as receiving a trait; as though traits were inherited as houses are inherited. But in many cases extrinsic factors lead the same potencies to different results. Among these cases is leukemia.

Measuring Intrinsic and Extrinsic Factors

The great problem is to disentangle the roles of two interacting variables, heredity and environment. To do this necessitates holding one constant, while varying the other. In man it is impossible to hold heredity constant; the only human traits whose heredity can be successfully studied are those depending on inherited potencies so powerful as to give virtually the same results under all conditions. In these cases the environment is effectively constant. However, the distribution of leukemia in human pedigrees tells us nothing about the roles of inherited potencies and extrinsic influences.

This limits the study to experimental animals, in which it is possible to secure very great genetic uniformity as well as comparatively constant environment. Long continued, uninterrupted inbreeding, with matings between



SLYE'S PEDIGREE OF MOUSE LEUKEMIA

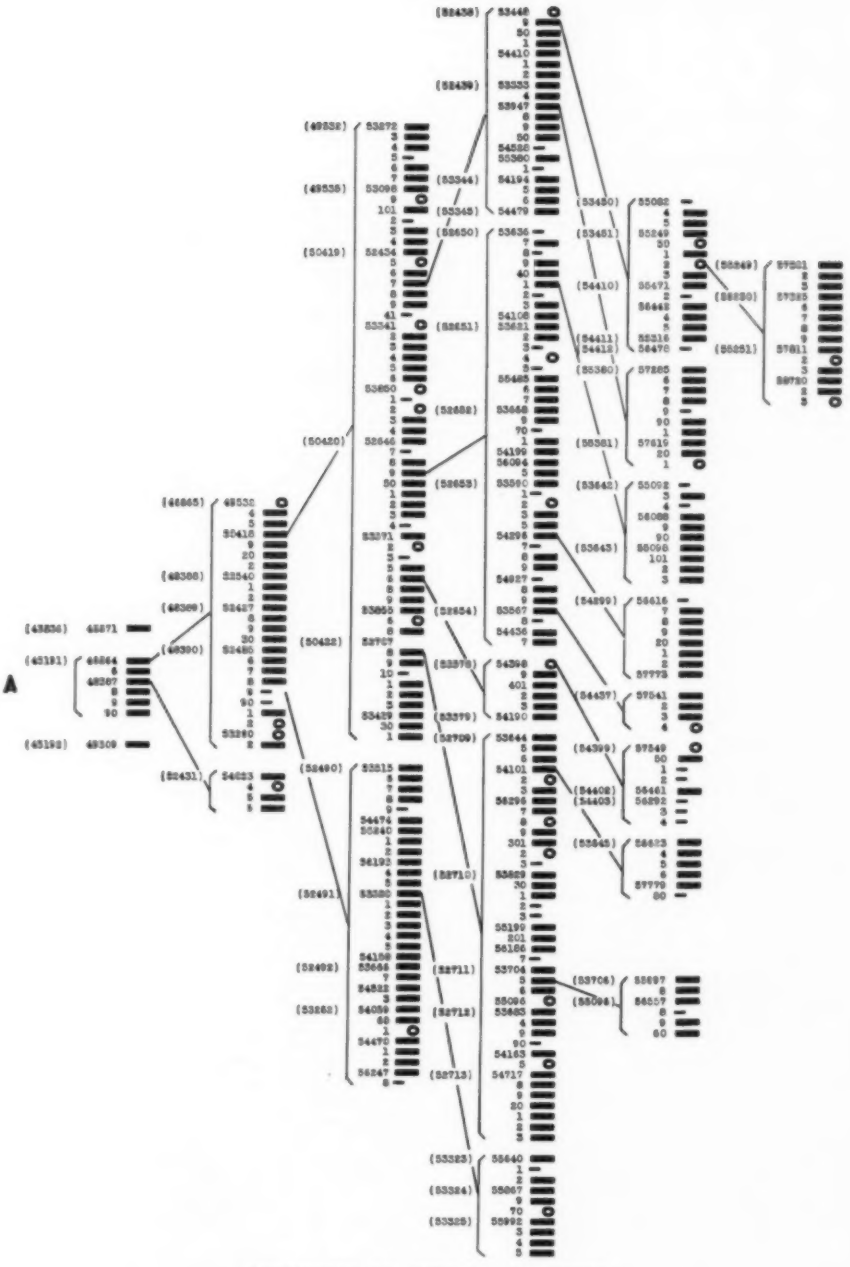
Figure 1

The high leukemia line was produced by three successive out-crosses, followed by inbreeding; note decrease in fertility accompanying increase in genetic homogeneity and increase in proportion of mice with leukemia. (Branches in which leukemia did not appear were omitted by Slye.) By the tenth inbred generation, the genetic variability was probably exceedingly small, but the number of mice is too small to eliminate an influence of non-genetic variables upon the incidence. Data from M. SLYE, *Amer. Jour. Cancer* 15: 1361-1386, 1931.

brother and sister, both establishes and maintains genetic uniformity within a strain. Such genetic uniformity reveals the fact that constancy of food and care and housing throughout a colony does not guarantee equal extrinsic conditions for all animals. For instance, the average litter size is different in different strains, yet the size of successive litters from the same mother is constantly varying. Heredity sets limits, but within these limits environment decides the size of each litter. Genetic uniformity may even reveal variations in extrinsic influences encountered by mouse embryos lying side by side in the same uterus. Thus, and here is the important point, constancy of extrinsic factors can not be taken for granted even in experimental animals, but must first be tested against constancy of genetic factors.

The first pedigree of mouse leukemia we owe to Slye (Fig. 1). The significant part of this pedigree consists of a series of generations of inbreeding with brother by sister matings, following three successive out crosses. During these generations of inbreeding the genetic variability was being automatically reduced; along with this, the incidence of leukemia increased until in the last generations all recorded animals exhibited leukemia. Unfortunately, with the inbreeding came infertility and the loss of the inbred strain just at the time a fairly high degree of genetic uniformity had probably been obtained. If, instead of three mice in the tenth generation, a few hundred could have been studied in this and subsequent generations, the influence of variations in extrinsic conditions might have been determined and a critical study begun. In the absence of a critical determination of the role of extrinsic factors, the various possible interpretations of these observations as they stand are purely formal.

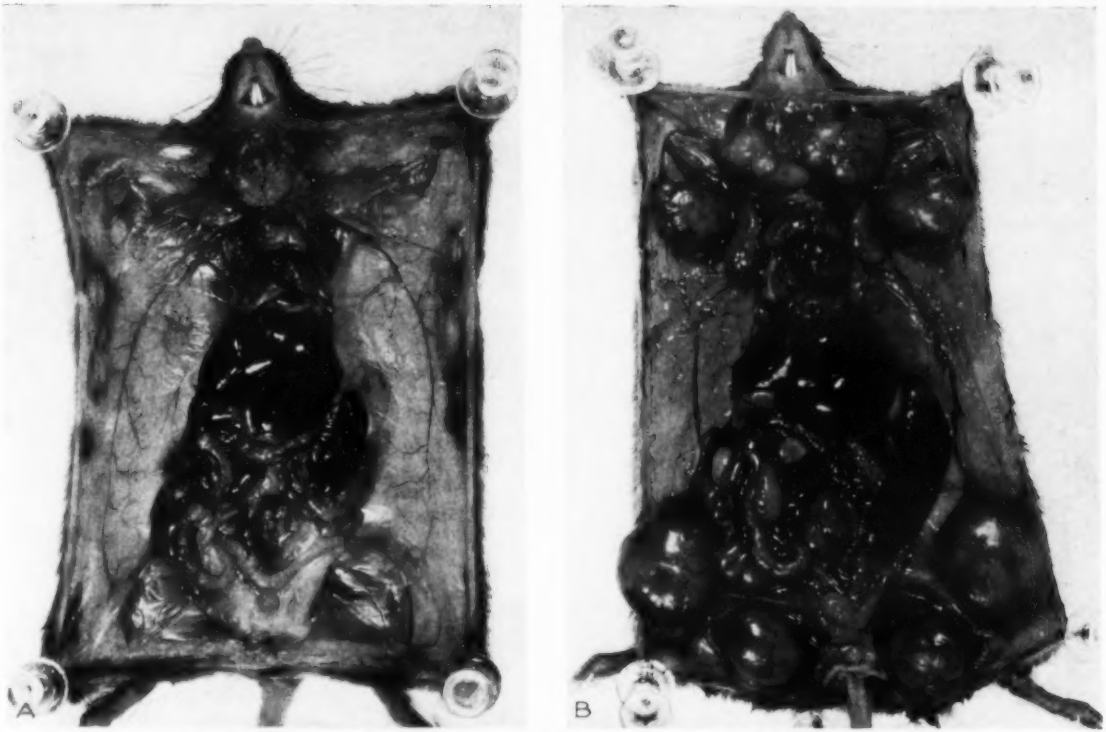
Another pedigree of mouse leukemia



A PEDIGREE OF MOUSE LEUKEMIA

Figure 2

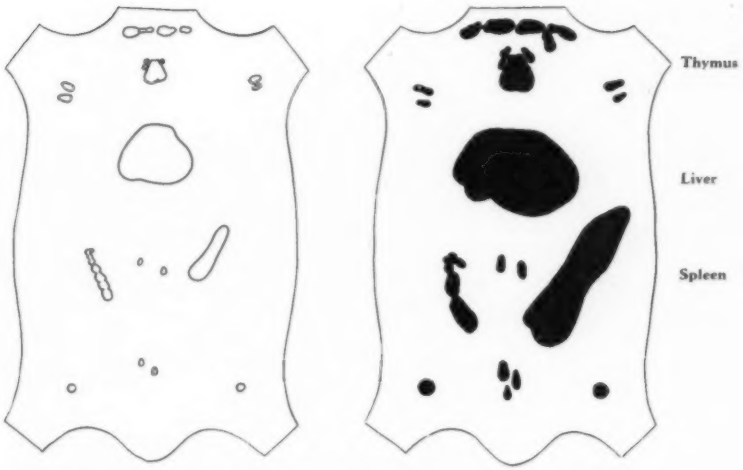
One of three branches of a pedigree of mouse leukemia that was preceded by 18 generations of brother by sister matings. *Heavy bar,* leukemia; *zero,* negative for leukemia; *dash,* diagnosis uncertain (mostly due to post mortem changes); lines connect fathers and their offspring; mothers, sisters of the fathers, indicated in brackets opposite first of young. In spite of genetic homogeneity, negative cases appear scattered at random through all three branches of the complete pedigree.



ANATOMICAL DIFFERENCES IN NORMAL AND LEUKEMIC MICE

Figure 3

A—Dissection of normal mouse showing normal spleen and certain lymph nodes, which have been separated from surrounding tissue. Nodes at knee and elbow (right of picture); mesenteric nodes, fused, at left opposite spleen; intestines moved to one side reveal lumbar nodes in center abdomen; mass at throat is mainly salivary glands with a row of lymph nodes along upper edge; thymus, above heart, carries one thoracic node on left margin (a bright dot). *B*—Autopsy of spontaneous leukemia (female 55269 2nd se. 301 days old). Body wall and ribs removed; excessive enlargement of superficial lymph nodes; nodes of throat, axilla and chest form pebble-like group about heart; deep nodes moderately enlarged; spleen, at right, typical enlargement; liver not enlarged. Different cases show great variation in distribution of tumorous enlargements.



OUTLINE DIAGRAM OF NORMAL AND LEUKEMIC MICE

Figure 4

Showing location of organs principally affected by leukemia. In this case there has been moderate enlargement of the lymph nodes and thymus, but very great enlargement of the liver and spleen. The organs of individual leukemic mice are affected to different degrees. Thus, in one case the spleen may be greatly enlarged and in another case the thymus, etc.

has been presented by MacDowell and Richter[1-3] (Figure 2). Here the observations were made on a strain that had previously been rendered genetically uniform by eighteen generations of brother by sister matings. In other words, this pedigree begins at a point eight generations beyond that at which Slye's pedigree ends. This pedigree shows a purely random sample of the mice of this strain that lived for more than six months. Two points stand out: first, many, but not all, developed leukemia; second, the negative cases are not due to family differences for they are distributed at random throughout the whole pedigree.

In a total of over six hundred, ten per cent failed to develop leukemia; yet the offspring of these negative mice developed leukemia as frequently as the offspring of leukemic parents. This demonstrates that all these mice were in fact genetically uniform. Why then do some of them escape having leukemia? You may suggest that these escaped by dying early from other causes. But this was not the case, for they happen to have lived unusually long lives. But it is also certain that the leukemic condition may appear at widely different ages; what is responsible for this variation? To answer with a question, What is responsible for the variations in the size of successive litters? Undoubtedly, variations in extrinsic influences.

This proportion of ten per cent negatives represents the balance between the genetic constitution of this particular strain and the particular range of extrinsic factors that they actually encountered. If the range of extrinsic factors were deliberately changed, or if the mice were moved to another laboratory, it is entirely possible that instead of one negative to nine leukemics, all might develop leukemia; or, again, negatives might appear in a much higher proportion.

ment of superficial lymph nodes; nodes of throat, axilla and chest form pebble-like group about heart; deep nodes moderately enlarged; spleen, at right, typical enlargement; liver not enlarged. Different cases show great variation in distribution of tumorous enlargements.

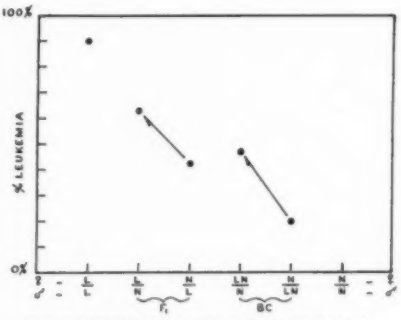
Given uniform heredity, the variation in performance is a measure of the variability of the significant extrinsic conditions. If we could provide all the mice of this strain with the extrinsic conditions met by those negatives, leukemia would never develop.

Under the actual conditions, the ten per cent negative cases is a reliable figure; the same proportion persists in successive random samples of the strain. With this relationship established, we are in a position to study the effect of hybridization on the incidence of leukemia. This strain was cross-bred to an equally inbred strain, which is called negative—as a matter of fact very exceptional cases of leukemia have been found.

Uniform Hybrids

If the heredity of a strain is uniform, all the germ cells will be the same, all will carry identical potencies. Thus when two such strains are crossed, all the offspring in the first generation necessarily carry the same combination of potencies. They are all hybrids, but equally hybrid. (This is true, of course, only in the first hybrid generation.) In this first hybrid generation there is no more genetic variation between different individuals than within either of the inbred parent strains. Therefore, the incidence of leukemia (for leukemia does appear) will give a measure of the variability of the extrinsic factors just as it did in the pure bred leukemic strain. And what is this incidence? What should we expect? Since half the heredity from the leukemic strain is enough to produce leukemia, and since the conditions necessary for leukemia to develop are met in nine cases out of ten, the incidence in this hybrid generation should be ninety per cent, the same as that in the pure strain. But this is not the case. With the leukemic heredity brought in by the father, the incidence is not far from forty-five per cent. What is wrong with our expectations? We assumed that the conditions necessary for leukemia to develop with all the leukemic heredity were the same as those required for leukemia to develop with half the leukemic heredity. This was wrong! The reduction of the leukemic heredity by a half, has reduced the number of cases by a half, because the extrinsic conditions required to produce leukemia with only half the heredity are not just the same and they occur much less frequently. These conditions are met only nine times out of twenty instead of nine times out of ten.

The reduced heredity requires more highly specialized conditions to reach the same end; the more specialized the requirements, the more effective the environment in controlling the outcome. In passing from one generation to the next, from a pure strain to the hybrid, the relative power of the given environment to prevent leukemia has been increased from one out of ten to five and one-half out of ten. There is nothing complicated about this once it is understood that we inherit only potencies. The weaker the potency, the stronger the outside help required to reach the same end.



DIFFERENCES IN RECIPROCAL CROSSES

Figure 3

Chart showing percentage of leukemia in two pure strains (L = leukemic; N = non-leukemic) and in reciprocal hybrids of F_1 and back-cross to N. In both generations the percentages are intermediate, but with leukemic heredity transmitted by females the percentage in each generation is significantly higher than when transmitted through males; the differences are respectively 4.5 and 7 times their probable errors.

LEUKEMIC GROWTH RUNS WILD IN A FAVORABLE ENVIRONMENT

Figure 6

Models of organs of mice showing the daily progress of leukemic enlargement of organs after transplantation of leukemic cells from another individual. Transplantation experiments have proven that the rapidity of growth of leukemic cells depends on the genetic constitution of the mouse which received the transplants as well as on the inherent nature of the leukemic cells themselves. A susceptible individual may be killed in less than a week by the wild growth of transplanted white blood cells, while a resistant individual will live much longer. Here we have again a demonstration of the balance between extrinsic and intrinsic factors which influence growth rates. The fact that transplants can be made, and that they flourish in a suitable "soil" proves that the leukemic cells themselves are different from the normal white blood cells, since they are able to "defy" the growth controlling mechanism adequate in the normal organism. Transplanted leukemic cells behave in the host like protozoan parasites. Merely a change in growth potency changes them from highly useful agents in the economy of the organism to a foe as deadly as the streptococcus.

Causes and Control

At this point I should like to pause a moment to consider two practical corollaries of this situation. One is an opportunity for study of environmental control; the other, a difficulty in the search for the specific genetic units.

First corollary: These first generation hybrids, normally meeting favorable and unfavorable conditions with nearly equal frequency, offer an excellent opportunity for the search for the significant extrinsic factors. From a medical standpoint, the possibility of manipulating extrinsic factors is the great hope; and it seems possible that the most important practical outcome of genetic study may not be the naming or enumerating of certain potencies or genetic units called genes, but the identification of important extrinsic factors.

Second corollary: Since the role of extrinsic factors differs as the heredity of the pure strain is divided, the second hybrid generation, in which all possible different combinations of genetic units occur, will present both unknown genetic variability and unknown variability of the effective extrinsic factors. The genetic variability can not be measured until the extrinsic variability is known. And the extrinsic variability can not be known until the genetic variability is measured. I think the difficulty will be admitted. On the other hand, the impression should not be given that this constitutes a theoretical impasse; by experimental breeding an analysis is possible, but practically the task of making such an analysis reaches staggering proportions. Unfortunately, such an analysis can not be reported for the present case.

This second corollary makes it clear that the incidence of leukemia in the second hybrid generation will not reveal the genetic formula. However, the incidence of leukemia in a back cross to the negative strain has been observed and may have some interest, even though interpretation is impossible. Crossing hybrid males back to the negative strain reduced the incidence of leu-

kemia to about one-half that in the first hybrid generation. Again the reduction of the leukemic heredity by one-half has reduced the incidence by about one-half. Thus with the leukemic heredity transmitted through fathers, in two hybrid generations, the incidence of leukemia is roughly proportional to the total heredity from the leukemic strain. This provides a fair prediction basis, but it does not provide any resemblance to a genetic interpretation in the modern sense.

After the discussion of reciprocal hybrids earlier in this program, it may be added that when the leukemic heredity is brought into the hybrids by mothers, the incidence in both first hybrid generation and in the back cross is again intermediate between the parental generations; but in both hybrid generations, the incidence is significantly higher when the mother brings in the leukemic heredity (Figure 5).

Intrinsic and extrinsic factors modify the incidence of leukemia; in two hybrid generations the incidence is reduced as the total heredity from the leukemic strain is reduced. The role of extrinsic factors is not constant, but varies with the intrinsic factors; thus the identification of the intrinsic factors becomes exceedingly difficult even in experimental animals; but in experimental animals it is possible to maintain intrinsic uniformity, and, therefore, to proceed with the search for the significant extrinsic factors, which, from a medical standpoint, offer the chief hope for practical application.

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3. Richter, M. N., and MacDowell, E. C. *Physiol. Revs.*, 15: 509-524, 1935.

◆

BREEDERS' GIFTS TO INDIA

WRITING of the moving of the Pusa Institute (India) to New Delhi, Dr. W. Burns records these significant contributions to agriculture from the first scientific breeding station established in India (*Nature*, London, March 13, 1937):

The Howards' wheats, particularly Pusa 4, Pusa 12 and Pusa 52, are now grown over six millions of acres in India, and some of the Pusa wheats have a vogue in Australia. Plant breeding for strictly economic ends and also the study of pure genetics have always figured largely on the programme of the Institute. Some useful hybrids between American and Indian tobaccos, wilt-resistant pigeon-pea strains, and better linseed types are some of the economic results, while the inheritance of characters in several important crops including linseed and chillies (Capsicum) has been the subject of important memoirs. It should be mentioned that the now world-famous Sugar Cane Research Station at Coimbatore in the Madras Presidency is a substation of the old Pusa and of the new Institute.

* * * *

No mention of the Institute would be complete without a mention of what is a great attraction to visitors, namely, the famous Pusa pedigree Sahiwal herd. This is one of the finest herds of milch cattle in India. It has been in existence since 1904, when fourteen cows and one bull were purchased from the Punjab. It has gradually been selected from homebred stock with occasional fresh blood from outside. The average milk yield per cow per day has risen from 5 lbs. in 1914 to 22 lbs. in 1934. The bringing of this herd, numbering 172, from Pusa to Delhi was an achievement in itself, a special train being required, taking four days on the journey. There was no break in the recording of milk yields or of the routine of the herd during the transit, and the animals arrived at Delhi in first-class condition.

A NEW CHROMOSOME MODEL

H. B. NEWCOMBE* and G. B. WILSON
Department of Genetics, McGill University, Montreal, Canada

CHROMOSOME models, used to demonstrate cytological crossing-over, have been made out of several materials. Chief among these are wool, plasticene, and pipe-cleaners. While useful models may be made with any of these none of them is ideal and all of them have at least one outstanding defect. The principal fault of wool and pipe-cleaner models is the difficulty of breaking and rejoining "chromatids." The inelasticity of the pipe-cleaners, while an advantage for static models, is a distinct disadvantage when studying the behavior of chromatids under the tension caused by their supposed tendency to coil or uncoil. Plasticene models also have this defect.

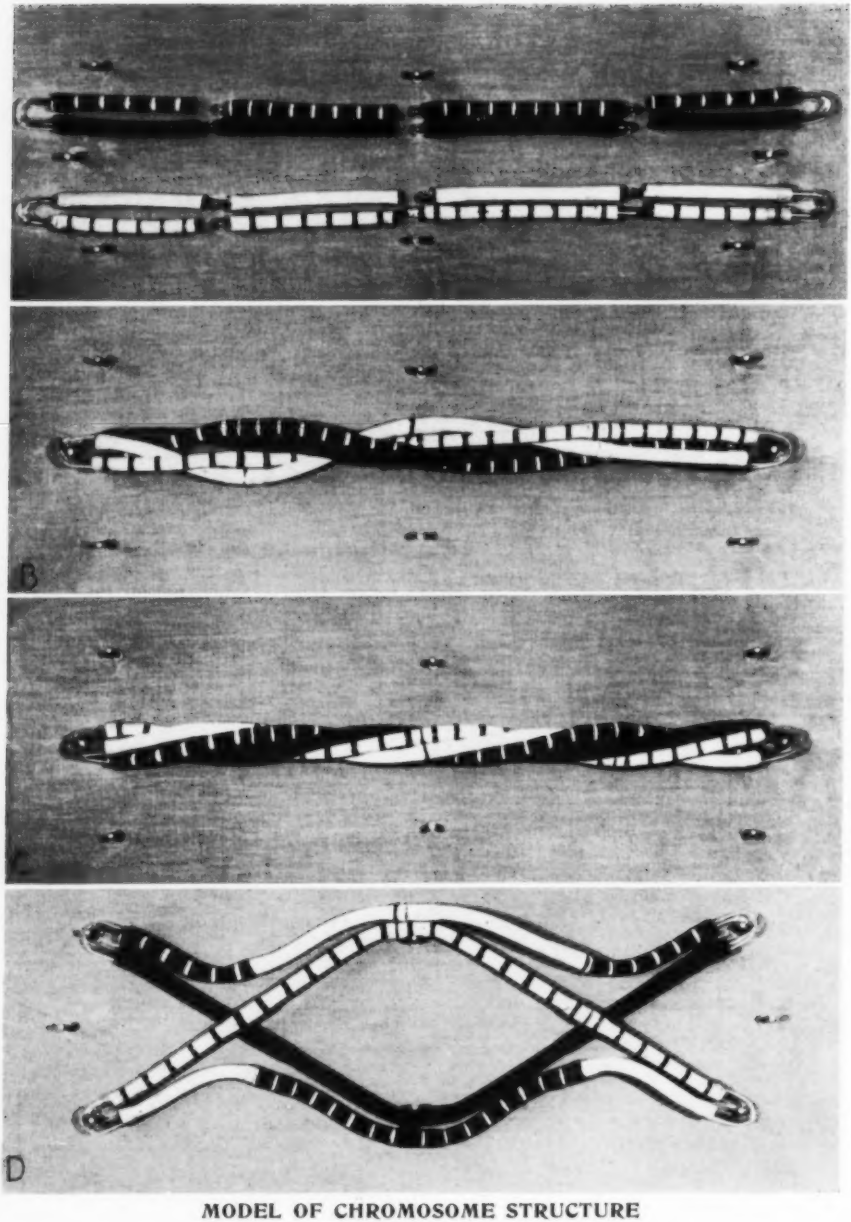
Since the most recent theories of the mechanism of crossing-over suggest that the chromosomes have a somewhat elastic nature, and possess an internal torsional strain at the time of chiasma formation, it seemed that rubber tubing was the best material for testing these theories. With this idea in mind, a simple model was evolved, as described below, which has proven very useful in this laboratory.

Four equal lengths of rubber tubing were painted different colors and taken to represent chromatids. Sister "chromatids" were joined at their ends by means of U shaped tubes. Each "chromatid" was cut into three parts and the cut ends rejoined by short lengths of glass tubing (Figure *7A*). One end of each piece was rounded so that it would easily pull out of the lumen of the tube. Then breaks were made at three points along each "chromatid;" thus the "chromatids" could be "broken" at these points and their free ends rejoined to form cross-overs. The entire model was mounted on a board in which nails were driven in such positions as to allow keeping the model in any desired shape. This simple model has all the advantages of the above mentioned models and lacks their most serious defects.

With continued use, several improvements have suggested themselves, which, if not increasing the actual efficiency, would, at least, improve the appearance and make it slightly easier to handle. A white board (painted or enameled) might make a better contrast with the model than an unpainted board. More important than this are the colors of the "chromatids." It seems more convenient to have sister strands of similar colors and "chromosomes" of distinctly contrasting colors; e. g. red and scarlet: white and grey. It may also be suggested that thick walled tubing is necessary in order to prevent collapsing when the "chromatids" are twisted. We have found too that it is better to glue in both ends of the U tubes as well as the unrounded end of each of the straight connecting-pieces to eliminate, as far as possible, unwanted breaks. Also, rubber bands may be used to hold "sister chromatids" together.

Such a model may be put to many uses. We have already used it in testing out current theories of crossing-over and chiasma formation and have found it very satisfactory. For instance, in testing the Darlington theory, the pairs of "chromatids" are first coiled independently in the same direction and then the "chromosomes" coiled about each other in the opposite direction (Figure *7B*). In testing the Wilson-Morgan (Sax) theory, the two pairs of "chromatids" are placed one upon the other and twisted so that all four remain parallel (Figure *7C*). In both cases breaks are made in the various possible ways, the

*Empire Cotton Growing Corporation scholar.



MODEL OF CHROMOSOME STRUCTURE

Figure 7

Painted rubber tubing and U-shaped glass connections make excellent material to demonstrate how rival theories account for the arrangement of chromatids in the chromosome. Details of structure are shown at *A*. Contrasts between the Darlington theory of chromatid arrangement (*B*) and the Wilson-Morgan theory of chromatid arrangement (*C*) are clearly shown by this model. The model is spread out to show details of behavior of the stretched chromatids at *D*.

ends rejoined according to their natural tendencies, and then the model is spread out by slipping the U tubes over the outside nails at the ends and the interstitial strands of the chiasmata over the two central nails (Figure 7*D*).

If, as some evidence suggests and these two theories postulate, chromatids have elasticity and a tendency to straighten out, thus causing torsional strain, the rubber "chromatids" may be expected to act in a somewhat similar way.

Also, we have found in our cytological work that drawings of chromosome configurations tend, in many cases, to be obscure and difficult to interpret due to the twisting of the chromosomes. By reproducing the observed configurations on the model and then straightening it out we have been able to get an accurate idea of the chromatid and chiasma relationships involved.

This model should also be useful for demonstration purposes. The ease and speed with which different configurations may be made gives it a distinct advantage (apart from its elasticity) over other commonly used models.

RUSSIAN PUBLICATIONS ON PLANT BREEDING

THE Soviet Union publishes through its Institute of Plant Industry, and through its *Selkhozgiz* — the Agricultural Press — a large number of reports, books, monographs on various phases of plant sciences, and in particular on plant breeding.

SELEKTZIA i SEMENOVODSTVO, or "Plant Breeding and Seed Growing," is a monthly publication, edited and published by the Commissariats of Agriculture, Soviet Farms (Sovkhoz) Food, and the Lenin's Academy of Agricultural Sciences, and as the name implies is devoted exclusively to problems of genetics, plant breeding, and seed production.

In the last three issues, there are several articles on the Hybrids of Wheat and Agropyrum and the Perennial Forms of Wheat. N. V. Tzitzin, the originator of these hybrids, gives a brief résumé of his work at the Siberian Institute of Grain Cultures at Omsk.

He describes his successful hybrids of wheat with *Agropyrum galaucum, Ag. trichophorum, Ag. junceum,* and *Ag. repens.* In 1936, he planted for the first time with grain drills 181 numbers of hybrids in two to four replications each. Extensive flour and bread baking tests with these hybrids were conducted. In his experiments with Triticum × agropyrum hybrids, Tzitzin has in mind five specific problems: 1. creation of drought resistant spring wheats; 2. creation of winter wheats equal to agropyrum in their cold resistance; 3. creation of alkali resistant spring and winter wheats; 4. creation of new forage crops, and 5. creation of perennial forms of wheat.

In addition to hybrids, the Station conducts work in producing new varieties of spring wheat, oats, barley, prosomillet, field peas, alfalfa and other grasses and forage crops.

A. I. Derjavin, of the Voroshilov Experimental Station, devoted specially to perennial crops, is another worker who has been developing perennial forms of cereal and other crops. He has an article entitled "Production of Perennial Forms of Wheat and Other Crops." He hybridized wheat with perennial forms of rye, also wheat with agropyrums, and selected perennial wheats among the wild specimens. The hybrid of Leucurum 1364/1 × *Secale montanum* produced perennial hard wheat. He has sufficient seeds of this hybrid on hand to plant five hectares this fall. Another successful hybrid was "Stepniachka" (wheat) × *S. montanum* (wild rye). Some of the best lines produced 39 and 49 seeds in a head, and weight of 1,000 grains

was 44.2 to 43.7 grams. He is also studying the perennial forms of rye, cotton, rice, and flax.

M. M. Sanmsonov has an article on "Quality of Grains in the Wheat-Agropyrum Hybrids." This is accompanied by pictures of loaves of bread baked from wheat and hybrid flours.

S. M. Verushkin describes some of the work at the Saratov Station with wheat-agropyrum hybrids under the title of, "Most Important Directions in the Work with Wheat-Agropyrum Hybrids at the Saratov Station." The work of the first successful wheat × Agropyrum hybrid was started by Tzitzin at this Station in 1930. Their tests proved that all hybrids were more frost resistant, more drought resistant, and more immune to rusts than wheat. He gives detailed charts showing the genom formulae, the scheme for exchange of homologic genoms, etc. They obtained four different groups: a 28 chromosome constant group; a 42 chromosome constant group; a 56 intermediate chromosome group, and a 70 chromosome amphidiploid group. The first two groups he considers as the most interesting from the point of view of developing perennial wheats.

Reports of the Omsk Meeting on Grain Crops, held under auspices of Lenin's Academy of Agricultural Sciences, will be shortly published. Also a recent meeting on problems of plant breeding, held in Moscow, at which Academician Lysenko and Academician N. I. Vavilov debated on some of the problems, will be fully reported in this publication.

J. W. Pincus
Consulting Agriculturist, Southbridge, Mass.

POLYPLOIDS IN PRACTICAL PLANT BREEDING

THIS clear and concise summary* the twenty-ninth in a series of booklets on fundamentals and advances in horticulture and viticulture, is the first treatment written in German to acquaint practical workers with the essential facts of cytology and plant breeding in relation to deciduous fruits.

Assuming no biological background on the part of the reader, the author describes in simple terms, illustrated by clear diagrams, the components of the cell, including within each chromosome the four chromonemata spirally wound and arranged in two pairs. Chromosomal synapsis is attributed to pairing of homologous genes. Disturbances of normal relationships may be due to presence of extra-chromosomal elements or to absence of elements normally present, to non-homology of the two haploid sets, to differences in gene arrangement, to haploidy, or to triploidy. In case of tetraploidy or hexaploidy pairing may be normal. Reduction phenomena in polyploids, including autosyndesis, allosyndesis and crossing over, with ratios obtained are described and various uses of autopolyploids and of allopolyploids in plant breeding are discussed. These general aspects of plant cytology, filling almost half of the booklet and accompanied my many practical suggestions, are lucidly presented. The non-technical reader is thus furnished with a key for understanding the facts applying to various species which are discussed and catalogued in the remaining pages.

The nine pages devoted to apples and pears tell the traits, breeding behaviour and origin of triploids with a list of diploid and of triploid varieties. Plums, cherries, peaches and apricots, chestnuts, hazelnuts and walnuts are briefly discussed. Cytology and genetics of berries, including raspberries, blackberries,

*Nebel, B. R., Zellforschung und Neuzüchtung beim Obst und dei der Rebe. Pp. 58. Figures 10. Grundlagen und Fortschritte im Garten- und Weinbau. No. 29. Eugen Ulmer, Stuttgart, 1936.

gooseberries and currants, and heredity of sex in strawberries and in grapes are reviewed. There are also given a list of plants with chromosomal races exhibiting phenotypic differences, a list of specific and generic crosses giving rise to new species and a discussion of artificial production of mutations and of chromosome doubling. The adaptive value of polyploidy to withstand northern climates, extreme salinity or other unfavorable conditions is presented with evidence from distributional studies.

It seems to the reviewer that the author has attained a comprehensiveness in this survey despite its compact form that should make the work invaluable for reference. Too bad for those unfamiliar with German that there is not an English translation.

P. W. WHITING
University of Pennsylvania

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ANIMAL WHO'S WHO

IT is fortunate that most of the tiny members of the clan of life such as Amoeba and Paramoecia could swim, or they would have had heavy going waiting hopefully all these years for the press of the Macmillan Company and the pen of Professor Hegner to serve as a "gangplank" whereby they could enter an ark. Some of the creatures depicted in Professor Hegner's paper-and-ink Ark* would have given old Noah quite a start if they had marched up the gangplank of the "Arrarat Special" with the alacrity with which they respond to the crack of Neo-Arker Hegner's pen. A protozoon occupying half a page would have given Noah no end of perplexity, which might have been forgotten when Ornythyrincus arrived, demanding classification as "fish, flesh, or fowl." The book is a fascinating pen and camera tour of the animate world which will be an inspiration to children and grown-ups alike. It should be very valuable in encouraging our own rather smug species in a much-needed wider interest in our friends, relatives, cooperators, and competitors in the fascinating game of life.

From the point of view of genetics the book presents little specialized material, though our old friend *D. melanogaster* is there with genes on. It also furnishes a remarkable array of illustrations of the amazing variety of forms and functions which have been evolved by living beings to solve the complicated problem of existence on this relatively tiny whirling speck of the Solar System on which we find ourselves in this Year of Grace, 1937.

A companion treatise to Dr. Hegner's book is found in a remarkable series of animal photographs recently issued by Charles Scribner's Sons.† This comprises a series of about 125 animal pictures selected from the International Exposition of Nature Photographers at the British Museum of 1935. The photographs were made by some eighty nature photographers in all parts of the world. The book is simply a series of portraits, the text being limited to a very brief introduction, a one-line caption under each "portrait," and the photographer's name.

The contrast between the almost technically perfect reproduction of these photographs, and the less refined paper and presswork used in "The

*HEGNER, ROBERT. Parade of the Animal Kingdom. Pp. 675. Illustrations, 743. Price, $5.00. New York: Macmillan Co. 1935.

†Nature in the Wild. Pp. 96. Price, $2.00. New York: Charles Scribner's Sons. 1936.

Hegner Ark" is an interesting study in publishing economics. Here the paper has been chosen as most suitable to reproduce half-tone illustrations, and the book is small enough so that the added weight and expense is not an overwhelming item. Had the "Ark" been published in the same format, the weight would have been only less appalling than the price, an excellent demonstration of the principle of mutual dependence which we find almost universal in life—from *H. sapiens'* printing industry to *Amoeba proteus'* behavior in a roadside puddle.

If one craves superb portraits of tigers, terns, bison, bull finches, and charging rhinoceri, *Nature in the Wild* is his book. It is curios that not a single anthropoid is to be found in the series. Thus if we yearn to bring our zoological portrait studies close home, phylogenetically speaking, it will be necessary to turn to Hegner's gallery, where an excellent series of monkey-pictures is to be found.

HOW WE CAME BY OUR BODIES

THE ostensible and avowed purpose of this book is to outline and discuss our knowledge and a few of our presumptions about the very important and barely explored country that lies in between biophysics, biochemistry, embryology and genetics. Around this nucleus, which lies in its proper position near the center of the unit, the author has built a considerable array of biological facts.

That the subject matter is important and timely may be further judged by a brief outline of it. There is some of the latest material upon the morphology of giant salivary chromosomes, modern theory of the chemical constitution of the gene, an outline of the elements of similarity in genes, enzymes and viruses together with a consideration of the role of genes and organizers in embryological development.

Offhand this might very well be considered rather high-powered material for even the upper third of the general reading public, the group for whom the text has been developed. The reviewer felt, therefore, that he was as much obligated to outline the methods the author uses to be easily intelligible as to summarize the matters covered.

One is struck immediately with the excellence of the illustrations taken from Maximow and Bloom, Arey, Cajal, Kollmann and other first-rate texts, generously supplemented with reproductions from anatomical periodicals, the Eugenics Record Office, and the JOURNAL OF HEREDITY. The illustrations are annotated with long explanatory legends which include synonyms of the technical terms employed. Taken alone the illustrations and legends constitute an impressive attempt to describe human structural and developmental details to the general reading public.

With the latter clientele in mind the text has been written with a minimum of technical words and where these occur explanatory interpolations are frequently introduced. In addition many analogies are made, some of the old faithful type but others sparkling with novelty, at least for the reviewer, who was particularly pleased with a comparison of red blood corpuscles and neuter social insects both wearing out for a group they can never add to.

Further reading material upon each chapter is itemized in a series of footnotes at the chapter's end. A glossary is combined with the index and the combination is very effective.

All this represents an effort that should elicit a favorable response in the reading public and for the most

DAVENPORT, CHAS. B. *How We Came by Our Bodies.* Pp. 401. Price $3.75. Henry Holt and Co., New York. 1936.

part has been accomplished without sacrifice of instructional essentials. However, the reviewer felt, in coming to the expressions, that the use of "innerskin" for entoderm would puzzle readers who are aware of an inner skin covering their own bodies, and that the use of "human egg" for early human embryo would complicate rather than simplify the description of cleavage and germ layer formation in human beings. Similarly among the list of very appropriate subtitles with which the text is generously supplied the use of "emergency department" for endocrine system too obviously connotes periodical rather than continuous endocrine control.

Part I, the entering wedge into the text material, is a description of human embryological development. This was a necessary prelude to any comments upon the role of the gene in character development, and balances what the author refers to as "sections which will appear speculative," with a considerable array of well authenticated and carefully illustrated facts. There is the added advantage that almost everybody would like some guidance in re-exploration of the narrow rugged path he himself has trod during his shadowy past.

The author particularly emphasizes during this description of ontogeny the fidelity with which the human embryo builds structures to fit itself for an environment it has yet had no experience with: "eyes but no light," "ears but nothing to hear." For the especial benefit of prospective parents development is carried past birth and up to "the adolescent explosion."

This section contains the only serious factual omission discovered. In the outline of the development of the eye, there is the statement: "The part of the pocket" (optic stalk) "next to the brain becomes narrowed to form the optic nerve." This omits the essential point, the growth back to the brain of the fibres of the ganglion cells. On the same page also there is an obvious confusion of cornea and sclera for author speaks of the "opaque white cornea of the eye."

Part II, which could have been as fittingly used for Part I, goes a little more fundamentally into the why of things and after an outline of the more important events of biological history presents well illustrated studies of cytology, histology and experimental embryology. The descriptive embryology of Part I here receives the discussion of the directive manipulations of genes and organizers. The author goes to some pains to illustrate also the kinship of genetics and embryology, disciplines which have in the past, too often acted like relatives who never visit one another and rarely speak unless cytology, which neither can do without, acts as a go-between. The discussion of the morphology of the cell is quite complete and includes illustrative material supplied by Metz, Painter, and Bridges. This is followed by discussion of the chemical constitution of the gene and hypothetical illustrations of how the genes may accomplish the work attributed to them. The author then takes up the important matter of cell position in the developing organism using the migration and group formations of mesenchyme cells for illustrative material with speculations upon their genic control and illustrations of the work of organizers in the production of certain characters in frog embryos and of the effects of mutual limb translocation between two species of Amblystoma. Part II is completed with a brief comment upon the effects of environmental differences as tested by identical twins.

Part III begins with some interesting speculation upon the genetic makeup of bacteriophage, viruses, bacteria and protozoa with the idea of accounting for gene origin and the origin of the nucleus and cytoplasm of the cell. The evolutionary discussion contains some points which are not presented with complete clearness. The author states on one occasion "But chance change in the gene has not been the sole directive force in evolution." It will not be apparent to a critical reader how chance change could be directive at all. Shortly thereafter the author states: "It ap-

pears, then, that some of man's genes are as old as organic life on earth though they have undergone change in number and quality." If genes are large molecules which can act as organic catalysts, the conception of them which has been presented to the reader, change in quality will be interpreted as involving change in molecular make-up and therefore the production of a new molecule which is only as old as the date of change.

The remainder of material in Part III consists largely of human genetics, a surprising amount of which is included in the 30 pages devoted to it. A general summary makes up the concluding presentation.

To end this review in similar style it can be said that the contained material is timely and organized in a novel manner, that the illustrations and explanations have been handled with skill, and that the fundamental value of modern genetics to any biological discussion is emphasized throughout.

R. R. HUESTIS.

University of Oregon.

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Books Received

BOOKS are acknowledged in this column as received, and such acknowledgment must be regarded as sufficient return for the courtesy of the sender. As far as space permits, books that contain material of special interest to the readers of the JOURNAL *will be reviewed in later numbers.*

FIFTY YEARS OF FIELD EXPERIMENTS AT THE WOBURN EXPERIMENTAL STATION, *by* SIR E. JOHN RUSSELL, D.Sc., F.R.S., and DR. J. A. VOELCKER, C.I.E., M.A. With a Statistical Report by W. G. Cochran, B.A. Pp. 392. Price, $7.50. New York, London, and Toronto: Longmans, Green and Co. 1936.

BIOLOGISCHE TYPEN DES MENCHEN und ihr Verhaltnis zu Rasse und Wert, *von* EDUARD ORTNER. Mit 70 Abbildungen. Pp. 104. Price, M. 7.50. Leipzig: Georg Thieme. 1937.

INTO THIS UNIVERSE, The Story of Human Birth, *by* ALAN FRANK GUTTMACHER, Associate in Obstetrics, Johns Hopkins University. New York: Viking Press. 1937.

PREPARATION OF SCIENTIFIC AND TECHNICAL PAPERS, *by* SAM F. TRELEASE and EMMA YULE. Third Edition. Pp. 125. Price, $1.50. Baltimore: Williams and Wilkins. 1936.

CALL FOR A NEW SOCIAL ORDER, *by* CHARLES FREMONT DIGHT, M.D. Pp. 181. Price, $1.00. Minneapolis, Minn.: Argus Publishing Co. 1936.

SCIENTIFIC PROGRESS, *by* SIR JAMES JEANS, SIR WILLIAM BRAGG, PROF. E. V. APPLETON, PROF. E. MELLANBY, PROF. J. B. S. HALDANE, PROF. JULIAN HUXLEY. Pp. 212. Price, $2.00. New York: Macmillan Co. 1936.

HUMAN GENETICS AND ITS SOCIAL IMPORT, *by* S. J. HOLMES, Professor of Zoology in the University of California. Pp. 414. New York and London: McGraw-Hill Book Co. 1936.

THE SOCIAL THOUGHT OF THE ANCIENT CIVILIZATIONS, *by* JOYCE O. HERTZLER, Professor of Sociology, University of Nebraska. Pp. 409. Price, $4.00. New York and London: McGraw-Hill Book Co. 1936.

PRINCIPLES OF TOPOLOGICAL PSYCHOLOGY, *by* KURT LEWIN, Professor of Child Psychology, Iowa Child Welfare Research Station, University of Iowa. Translated by Fritz Heider and Grace Heider. Pp. 231. Price, $2.50. New York: McGraw-Hill Book Co. 1936.

THEORY AND PRACTICE OF PSYCHIATRY, *by* DR. WILLIAM S. SADLER. Pp. 1231. Price, $10.00. St. Louis: C. V. Mosby Co. 1936.

INSTITUTIONAL TREATMENT OF DELINQUENT BOYS, Part 2—A Study of 751 Boys. United States Department of Labor, Children's Bureau, Publication No. 230. *By* ALIDA C. BOWLER and RUTH S. BLOODGOOD. Washington: U. S. Government Printing Office. 1936.

SEX EDUCATION, *by* MAURICE A. BIGELOW, Professor of Biology and Director of the Institute of Practical Science Research, Teachers College, Columbia University. Revised Edition. Pp. 307. Price, $1.00. New York: The American Social Hygiene Association. 1936.

PSYCHOLOGY AND THE SOCIAL ORDER, An Introduction to the Dynamic Study of Social Fields, *by* J. F. BROWN, Ph.D., Associate Professor of Psychology at the University of Kansas. Pp. 529. Price, $3.50. New York and London: McGraw-Hill Book Company, Inc. 1936.

FINGER, PALM AND SOLE PRINTS OF MONOZYGOTIC QUADRUPLETS

JOHN W. MACARTHUR
University of Toronto
and
O. T. MACARTHUR

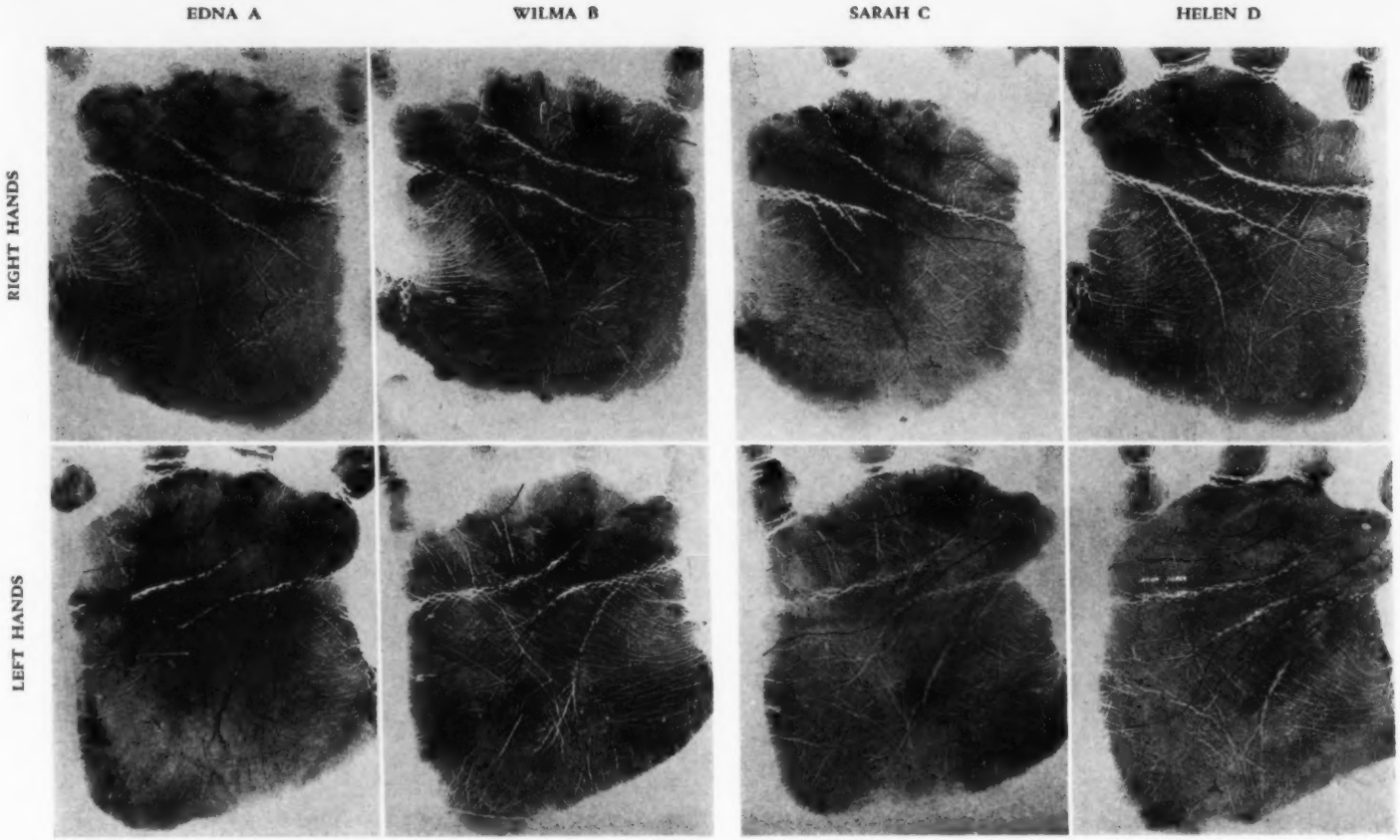
Wide World Photo

THE MORLOK QUADRUPLETS ON THEIR FIFTH BIRTHDAY

Figure 8

Edna A, Wilma B, Helen D, and Sarah C, alike as babies, resemble each other no less closely at the end of five years.

IN this JOURNAL (July 1932) appeared Dr. A. E. Clarke's account of the Morlok quadruplets. He reviewed their history to eight months of age and judged them probably monozygotic from the placental findings, the general close resemblance in features and other physical characters, and from the



PALM PRINTS SHOW CROSS RESEMBLANCE

Figure 9

Differences in development of a fundamental pattern rather than any great variety in patterns, is the impression given by the palm prints. Mirror imaging is often associated with identical twinning, and some of the patterns give striking examples of this phenomenon. Thus the right hand of *B* in several features is a mirror image of the left hand of *C*. The crease patterns as well as the friction ridge patterns show striking mirror image resemblances. Frequently the palm prints of twins show greater cross resemblance than resemblance between right and left hands of one member of the pair. This is true in several cases in this group.

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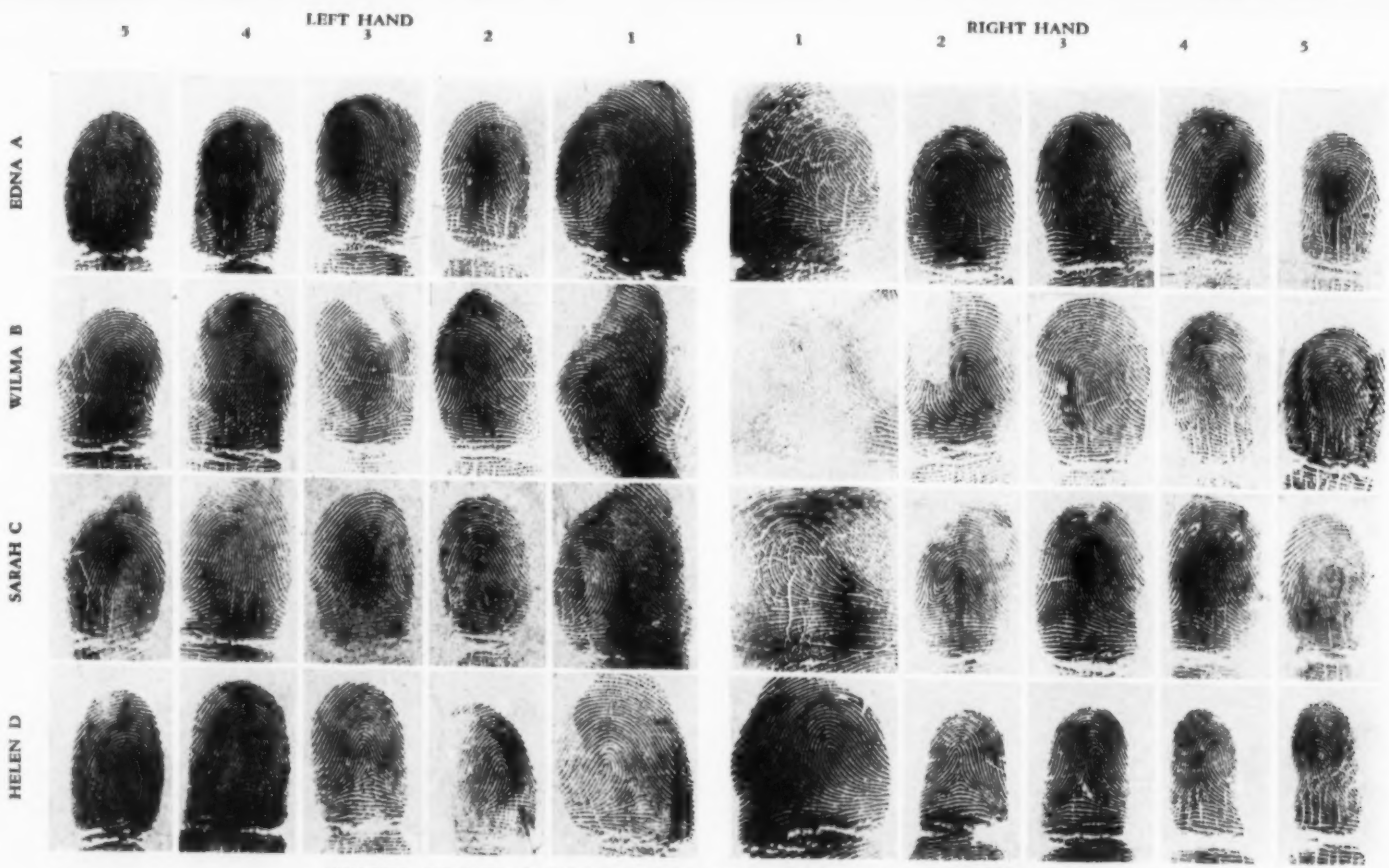
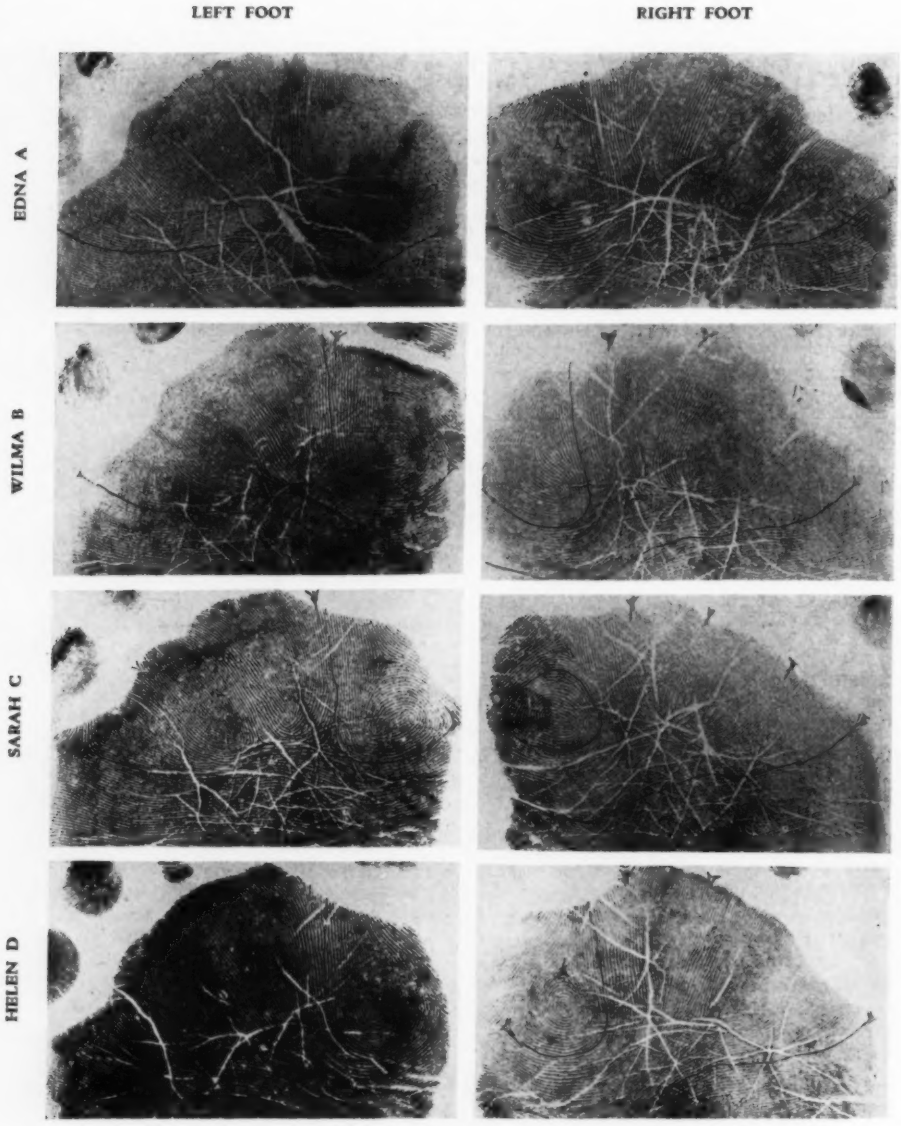


FINGER PRINTS SHOW RESEMBLANCE WITH SMALL DIFFERENCES

Figure 10

The finger prints are not as much alike as are the finger prints in some pairs of identical twins. They are much more alike than we would expect the finger prints of fraternal twins or of four ordinary brothers or sisters to be. When mirror imaging is taken into account some rather remarkable resemblances can be noted. There is no clearly marked differentiation of the twins into two or more groups on the basis of finger print patterns. There is rather a series of "links of cross resemblance" which is convincing evidence that the twins are genetically identical.



FOOTPRINTS SIMILAR IN MAIN PATTERN FEATURES

Figure 11

While none of the footprint patterns is exactly like any of the others, there is a rather remarkable general resemblance, with striking cross resemblances between some of the prints, especially if we consider the mirror image relations often seen in twins. Thus the right feet of *A* and of *D* have a remarkable mirror image resemblance to the left foot of *C*. The left feet of *A*, *B*, and *D* are also notably alike and the other cross resemblances can be noted. Such interlocking cross similarities make it impossible to separate the quadruplets into "pairs of identical twins" or into "triplets and a sister."

Derby Studio

MORE ALIKE THAN THEIR FINGER PRINTS

Figure 12

The expressions of Edna A, Sarah C, Wilma B, and Helen D, Morlok are rather more different in this picture than usual, but the four girls are not so very unlike each other for all that. In height the quadruplets vary at present from 41½ inches (*B*) to 43 inches (*A* and *C*). There is a difference of one full size in the shoes worn by the largest and smallest of the quadruplets. They show at least two usually recessive characters exhibited by one parent and not by the other (straight blond hair vs. curly dark hair). The chance that all the quadruplets would show this combination were none of them identical is 1 in 256. This alone is suggests strongly that they have arisen from a single fertilized egg, and if the probability that other traits would also show no deviation were included, very significant evidence of identity would be adduced.

somewhat fragmentary finger and palm print data. Because such cases are rare and of much scientific interest, additional notes on this family and particularly a more satisfactory dermatoglyphic record of the set at six years and two months are here presented.

The conclusion that this set has originated from a single egg seems fully warranted. The four girls are practically quadruplicates in a great number of characters: they all have dark hazel eyes quite precisely matched both in color and patterns, the same long dark brown lashes, very fair complexion, and straight fair hair. The hair now resembles the father's, the mother's being dark and curly. The ears are remarkably similar and have the lobe free as in the mother, not attached as in the father. Other noticeable features are the breadth of the nose at the root, the similarity of the teeth, the lateral extent of the mouth and jaw, and the habitual slight parting of the rather thin lips. A first impression is that one might learn to distinguish them by the somewhat rounder faces of A and D, and by the still marked (but apparently diminishing) differences in sizes; A and C are tallest (43") and wear size 9½ shoes, while B's height is 42½" and D's 41½", both the latter taking 8½ shoes. All, including the parents, were found to be non-tasters of P.T.C. Pryor reports the further remarkable fact that each of the four shows the same exceedingly rare condition of having an extra proximal epiphysis on the second metacarpal of each hand.

The mother emphasizes the girls' individuality in disposition, regards A as the leader, and believes A and C to be paired off against B and D in interests and actions. To new acquaintances, however, they seem in these respects indistinguishable, similarly alert and intelligent; they are considered equally capable in school work and similar in musical gifts (a Seashore test would be of interest).

Dermatoglyphics

The readings of the hand and foot prints have in all cases been checked from several extra printings, on the basis of which we venture to correct and extend the earlier formulations. The tracings are intentionally minimal. In general the papillary patterns are comparatively reduced on both hands and feet.

The fingers nearly all bear ulnar loops or some closely related pattern (Figure 10), the most exceptional being the index fingers of A and C, which carry radial loops on the left and a type approaching double loop whorls on the right. The pattern shape is elliptic, the index by Bonnevie's revised method averaging nearly 60. Ridge counts (quantitative value totals for left and right hands by Newman's classing method) are rather similar in A (29-32), B (29-34) and C (28-31), but decidedly lower in D (21-23) (see Table I). Apical patterns were also recorded as read with a lens directly from the inked toes. These patterns too are predominantly "ulnar" loops and have very low ridge counts, notably on the left feet of A and

Table I. Finger patterns classed as by Newman, and ridge counts read from left to right, with total quantitative value (Q.V.)

	Left fingers						Right fingers					
	5	4	3	2	1	Q.V.	1	2	3	4	5	
A	U 0-8	U 0-14	U 0-10	R 4-0	U 0-12	L. 29	R. 32	U 12-0	Mdr 9-5	U 10-0	U 9-0	U 11-0
B	U 0-9	U 0-11	U 0-11	U 0-3	U 0-10	29	34	U 11-0	U 13-0	U 11-0	U 16-0	U 7-0
C	U 0-6	U 0-15	U 0-9	R 8-0	U 0-15	28	31	U 16-0	Mdr 6-0	U 11-0	U 11-0	U 7-0
D	U 0-10	U 0-3	U 0-3	U 0-4	U 0-9	21	23	U 11-0	R 0-3	U 9-0	U* 7-0	U 6-0

Table II. Toe patterns and ridge counts as (approximately) read by direct examination. In this table U stands for F (fibular) and R for T (tibial) patterns.

	Left toes						Right toes					
	5	4	3	2	1	C.V.	1	2	3	4	5	
A	U 0-8	T.A.	U 0-3	T.A.	U 0-11	L. 16	R. 22	R 6-6	U 7-0	U 7-0	U 6-0	U 8-0
B	U 0-7	U 0-9	U 0-6	U 0-1	U 0-4	19	27	U 4-0	U 10-0	U 14-0	U 11-0	U 4-0
C	U 0-6	U 0-6	U 0-4	U 0-8	U 0-9	22	26	U 7-0	U 8-0	U 12-0	U 6-0	U 8-0
D	R 8-0	T.A.	U 0-8	A	U 0-5	18	26	U 11-0	U 9-0	U 9-0	U 8-0	U 4-0

Table III. Palm Formulae

	Left hands	Right hands
A	9 .0.5*.4 -t'- A^{B}/t^{E}.0.0.V.D.	11. 9(10).7(8). 5' -tt'- A^{B}/t^{E}.0.V.L.V.
B	9-7.0.5*.3 -tt'- A^{B}/t^{E}.0.0.V.D.	9. 0. 8*. 5' -t- A^{B}. 0.0.V.V.
C	9-7.9.5*.4 -tt'- A^{B}/t^{E}.0.0.L.D.	9(10).0. 5*(6).5' -t- A^{B}. 0.0.V.V.
D	9. 0.5*.3 -t- A^{B}. 0.0.V.V.	11. 0. 7. 4 -t'- A^{B}/t^{E}.0.0.V.V.

Table IV. Foot Patterns recorded after the method of Thorsten Lund in the order: hypothenar, calcar, thenar, hallucal, the three plantar interdigitals; and plantar deltae (d)

	Left feet	Right feet
A	0.0.0.L^{d}.0. L^{d}. 0. d	0.0.0.W. 0.L^{d}. 0. d
B	0.0.0.W. 0. $L^{d}V$.0.	0.0.0.L^{id}.0.L^{d}. 0. d
C	0.0.0.W. $L^{d}.L^{d}$. 0. dd	0.0.0.W. 0.L^{d}. 0. d
D	0.0.0.L^{d}.0. $L^{d}V$.0.	0.0.0.W. 0.$L^{d}V$.0.

D where the loops pass over transitionally toward arches on digits II and IV (Table II).

The palm prints show a strong resemblance in a number of features: triradius *c* is absent from all the hands, except A's right and C's left; the basic line formula of left hands is 9.0.5.3; axial triradii, tt', enclose a hypothenar ulnar loop in one hand or the other of all but D; and the outer interdigital patterns are similar in their reduction and in many details on all the right hands. In palm prints B and C may be said to be most alike, especially in the right hand palms, whose line terminations are like those of the left side, a state that may be interpreted as a partial mirror image reversal (Figure 9).

The foot prints were completed by rolling in the hypothenar, calcar and thenar regions; since these patterns are evidently wholly missing on all the feet, only the plantar areas are published (Figure 10). Not all the subdigital triradii were reached even on the extra prints. There is some resemblance in the line courses and in the patterns; each individual has one or two hallucal whorls, and the middle plantar is represented by either a loop opening distally (L^4) or a distinct vestige of it (L^4V). On the whole the feet are most alike in the patterns absent, and differ rather markedly in the number of plantar deltas, in the patterns found, and in such of the lines as can be traced.

It is to be particularly emphasized that no one of the four stands apart as an odd one, nor do any two of them pair off consistently from the others, in all respects. A and C are most alike in finger patterns, B and C in toe patterns and palms, A and B in sole patterns; D stands somewhat apart in finger ridge counts, but both A and D have low values in the toes. Even these likenesses are rather between two or more hands or feet (of the same or opposite sides) than between two individuals as a whole.

By a quantitative method being described elsewhere the average difference in seven respects (ridge counts and patterns of fingers and of toes, palm lines and patterns, and sole patterns) is 28 per cent between the left and right sides of the four individuals, while the same-side hands and feet of the set differ by 22 per cent. Thus the method of Komai and Newman confirms the diagnosis of monozygosity. Moreover, when these quadruplets are considered and compared as if they were six pairs of twins, they were found to differ only slightly more than do the average of seventy pairs of identical twins, and decidedly less than the average of as many fraternal twins.

In general, while the dermatoglyphics are not so strikingly similar throughout as to practically prove monozygosity independently of other criteria, the study as a whole leaves no real doubt that the set is uniovular.

POSTPONEMENT OF GENETICS CONGRESS

THE VIIth International Genetics Congress which was going to be held at Moscow, U. S. S. R., this summer has been postponed. According to the information received from the Organization Committee, a number of scientists and institutes have requested this as they wished to be better prepared for the congress. The Academy of Sciences and the Organization Committee have now extended an invitation to hold the congress in Moscow in August, 1938. Conforming with the mandate given to the Permanent International Committee for Genetics Congresses, the entire matter will be put before this committee for decision. At present it is certain that no International Genetics Congress will be held in 1937.

OTTO LOUIS MOHR
Chairman of the International Committee

A GENETIC HISTORY OF THE BROWN SWISS CATTLE IN THE UNITED STATES*

DORSA M. YODER and JAY L. LUSH

THE first Brown Swiss cattle were brought to this country in 1869. The last importation came in 1906. Altogether only 21 males and 129 females were imported.† The Brown Swiss cattle breeders' association was established in 1880 and has registered over 50,000 females and 30,000 males, descended entirely from those 150 imported animals. The 1930 U. S. Census enumerated 25,734 purebred Brown Swiss cattle alive that year. Since 1906 this breed, which previously had been classed as dual-purpose, has been entered in the shows and judged as a dairy type. The Register of Production was established in 1911 and 1,317 cows had been entered by 1933. The cows in the yearly test have averaged 540.2 pounds of butterfat.

A study of the breeding practices in the Brown Swiss breed was undertaken because of personal interest in learning more about its history and because the small number of animals originally imported made it seem likely that there would have been in this bred some unusually interesting genetic situations.

We wished most to know how much inbreeding there had been in the development of this breed and whether such inbreeding had happened incidentally from the small number of foundation animals, or from deliberate linebreeding to certain animals or families, or from still other breeding systems, and whether certain individual ancestors had been vastly more important than others in making the genes of the breed what they are today.

Methods Used

Systematic samples of 400 pedigrees to represent the whole breed at different dates were selected from the Herd Book, in a predetermined manner, regardless of the name of the breeder or the name or number of the animal. The Register of Production sample was gathered by taking about one-third of the cows with highest records in each Register of Production class without duplication of name or record. For the sample of prize winners at shows, the National Dairy Show and the Dairy Cattle Congress were each sampled for five years by taking the highest five placings in the mature classes. For four years the three highest placings in each class at three of the Mid-west state fairs where many Brown Swiss are usually shown were included. One other Mid-west fair was similarly sampled for three years, and two were sampled for one year. The Eastern States Exposition was sampled for four years and the New York State Fair and the Trenton, New Jersey, State Fair were used for one year each. In the far west the Pacific International was sampled one year. Duplication of animals was avoided. There were 365 pedigrees in this show sample.

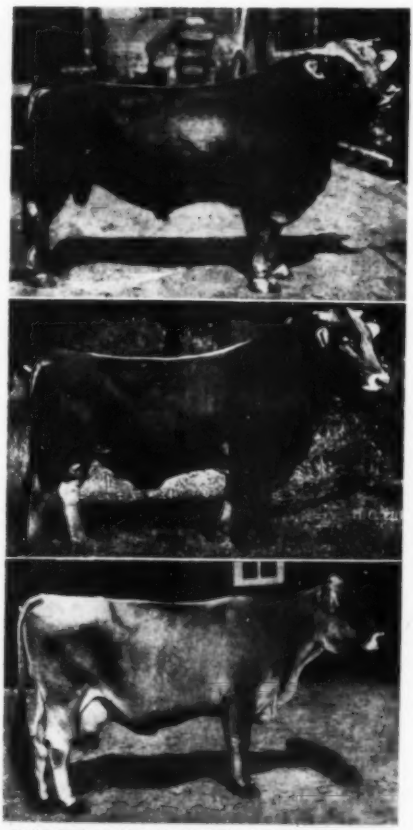
Two-line pedigrees were then traced at random for every animal in each of the above samples. Relationship and inbreeding coefficients were computed by the short methods developed by Wright and McPhee[6]. Card sorting and tabulating machines were used to count the number of appearances of each ancestor.

Animals Which Have Had Most Influence on the Breed

All animals which appeared 20 or more times in two or more samples or 30 times in one sample are listed in Ta-

*Journal Paper No. J-412, from the Iowa Agricultural Experiment Station.

†A small importation not included in these figures was made through Mexico in 1931 but that was since the birth of the youngest animals included in this study.



THREE IMPORTANT MEMBERS OF THE BROWN SWISS BREED

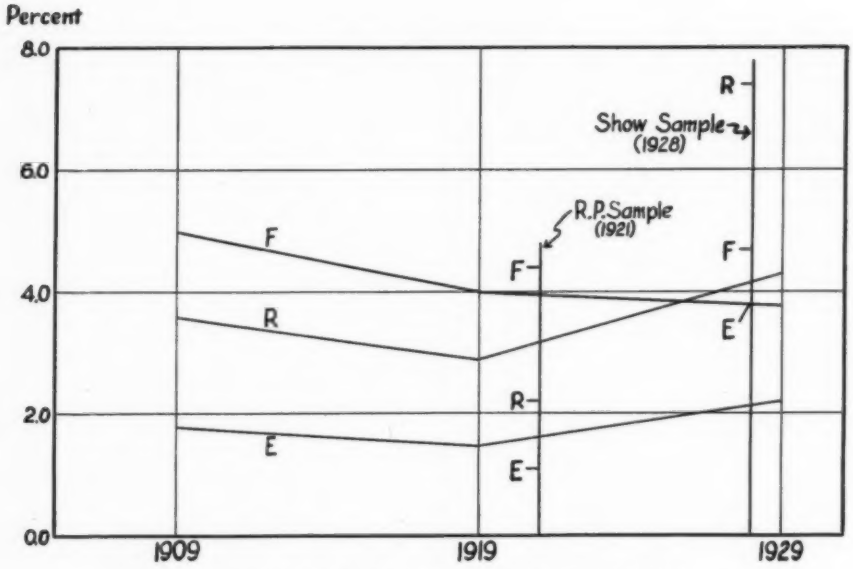
Figure 13

Junker (*A*), imported in 1906, is the most frequently found bull in the Register of Production and Show Groups, being exceeded by William Tell (the original Swiss bull imported into the U.S.) in the breed at large. Junker's son, Reuben (*B*), has also had a prominent place in the gene-history of the breed. College Bravura 2nd (*C*) is prominent among the eight females which appeared twenty or more times in at least two of the groups. She had a record of 19,460.6 pounds of milk, and 798.16 pounds of butterfat. No single animal has ever dominated the Brown Swiss breed in the United States. Inbreeding has not been extensively practiced.

ble I. The standard errors of these numbers are about 5 for numbers from 20 to 30 and about 6 for numbers from 30 to 45. William Tell, the first bull imported, leads all animals with 75 out of 800 possible appearances in the 1909 sample. Junker, a bull imported in 1906, comes next, even surpassing William Tell in the Register of Production and Show groups. If Junker had come at an earlier date in the breed's history, would his influence on the breed have been greater? Another sire to surpass William Tell in the later samples is Bonaparte, who was imported a generation or so after the first importation. Reuben and Zell, who appear often in all but the earliest sample, were both sons of Junker. Zell attained early fame on the show circuit and had his popularity established early enough to appear 16 times in the 1909 sample. Reuben surpassed Zell in his number of appearances only in the Production Group. College Boy and his sire, Carl, appear often in the later groups and are especially prominent in the Show group.

Eight females appeared 20 or more times in at least two groups. The cow Schoni passed her influence mostly through her son Burleigh and grandson Santa Claus which was 12.5 per cent inbred to Bonaparte. College Boy, one of the more prominent later sires, has in his pedigree the cows College Bravura 2nd, Bertha M. and Cuma. Cuma was 21 per cent inbred, mostly to Duke of Iroquois, Black Eagle and Don Fritz Burgi. Bertha M., prominent among later cows, exerted her influence mostly through her sons, College Boy and College Carl.

Perhaps the most significant fact from Table I is that the highest number recorded there, the 75 appearances of William Tell in the 1909 sample, indicates that no one animal contributed more than about 9 per cent of the genes of the breed. (Probably even this figure is a little too high on account of sampling errors, since the 75 was picked out for illustration here because it *was* the highest figure found). This figure may be helpful as a crude yardstick against which to check qualitative statements about how very much a breed was in-



INBREEDING AND RELATIONSHIP COEFFICIENTS

Figure 14

Average actual inbreeding (F) and *inter se* relationship (R) and inbreeding expected from *inter se* relationship if breeding had been random with respect to pedigrees (E) in the Brown Swiss breed. The coefficients show that the breed as a whole has not been intensely inbred since its introduction into the United Staees.

fluenced by some prominent animal. But another important side of this story is that if each of several foundation animals, not closely related to each other, contributed several per cent of the genes of the breed, then such a small group furnished a large part of the inheritance of the breed. The reasons or accidents which led to the prominent use of these particular animals, instead of their contemporaries, may have caused the frequencies of certain genes to wander far from what they were in the population from which the foundation animals came. So far as those choices were based on deliberate reasons, this changing of gene frequencies is *selection* and would be a force of about equal power whether there were many or few animals in this foundation group. But so far as those decisions were random accidents, as likely to select for a gene as against it, the process of changing gene frequencies acts the same as inbreeding and this is a much greater force for change when there are few animals in the foundation group than when there are many. The sampling variations in gene frequency being random *tend* to cancel each other. The extent to which that happens is greater as the number of foundation animals increases from a few important ones to many, each of which is of little importance by itself.

Data from the 1929 sample may be used to illustrate the point. Not as many as 8 per cent of the random lines ended in any one foundation animal. Yet more than one-fourth of the lines ended in five foundation animals, more than half of them ended in 13 and more than three-fourths of them ended in the 29 more frequently found ancestors. The same five foundation animals from which

came 218 of the 800 random lines in the 1929 sample were at the ends of 219 lines in the 1919 sample and 213 lines in the 1909 sample. It appears likely that their influence is so evenly distributed through the breed that it can scarcely be changed now by selecting for or against pedigrees in which they occur. The 13 foundation animals from which came 402 lines in the 1929 sample were the source of 378 and 366 lines in the 1919 and 1909 samples, respectively. The 29 animals from which came 603 lines in the 1929 sample were the source of 545 lines and 565 lines in the 1919 and 1909 samples, respectively. With such a large proportion of the genes of the breed coming from such a small group of animals, chance (which to some extent determined that those particular animals should have played so large a part) must have had much to do with determining the gene frequencies which characterize the breed today.

The comparative relationship of the foundation animals to the whole group is indicated by the number of appearances shown for each of them in Table I, but the later animals may have much collateral relationship to the group through having important brothers, sisters, aunts, uncles, etc. The highest individual relationships to the samples of the whole breed were 9.2 per cent for William Tell in 1909 and 9.1 per cent for College Boy in 1929. The highest relationships for cows were 8.6 per cent for Josie in 1909 and 7.4 per cent for Bertha M. in 1929. Several other males were above 5 per cent and several other females were above 3 per cent. The Production sample differed little from the 1929 sample in the closeness of its relation to the prominent animals. But among the more recent ancestors there were several which were much more closely related to the Show sample than to any of the other samples. This may be due to the customs involved in showing. Only a few herds make a regular practice of showing large numbers at the major fairs. Whatever sires are used extensively in those herds have considerable chance of appearing frequently in the pedigrees of a sample of show winners. Testing for production is by no means as nearly confined to a few herds which specialize in it as is the showing at large state and national fairs.

Amount of Inbreeding

The inbreeding coefficients found are shown in Table II and Figure 14. The interval from 1909 to 1929 is so short—only about four cattle generations in length—that a trend could hardly be

Table I. Number of times the more prominent animals were found in each sample

	Year of birth	Registration Number	Kind of sample				
			1909	1919	1929	Show	R.O.P.
Males:							
William Tell	1888	1	75	63	43	31	37
Albert Tell	1870	2	37	30	21	13	19
Ivernese Tell	1873	11	21	20	19	9	15
Frederick Schiller	1880	115	47	32	33	32	36
Bompartz	1883	141	48	48	46	38	39
Iroquois	1884	197	30	30	29	16	28
Burleigh	1898	344	34	31	30	33	41
Francis B	1888	386	34	21	30	23	25
Bonafide	1890	456	30	38	34	38	36
Werner Steuffacher	1889	466	15	15	24	27	23
Santa Claus	1889	497	25	21	34	28	24
Grover Blanc	1898	597	21	16	25	20	28
Benny Blanc	1896	739	18	19	20	15	24
McKim	1898	1120	34	38	37	18	36
Edgard	1902	1817	0	18	22	27	26
Junker	1904	2345	16	44	61	47	38
Zell	1907	2818	16	22	38	43	34
Reuben	1909	2927	0	12	20	31	45
Carl	1911	3577	0	10	24	21	32
College Boy	1915	4316	0	11	35	49	37
College Carl	1914	4534	0	8	10	30	19
Vogel's College Boy	1915	5430	0	5	21	30	20
Vronicka's College Boy	1918	6736	0	0	9	21	7
Females:							
Brinlie	1887	4	28	20	20	13	20
Bide Rex	1892	207	27	30	35	14	16
Schoni	1879	252	27	16	28	12	16
Ida Burgi	1885	286	15	21	20	22	14
Cinder	1895	995	20	24	19	9	20
Cuma	1900	2198	1	12	12	28	21
College Brewers 2d	1901	2277	3	18	23	45	34
Bertha M	1907	4386	1	14	30	32	32
Cinnamon's Brownie	1914	7565	0	0	2	33	2
Number of random lines traced:			800	800	800	758	800

Table II. Inbreeding and Inter se Relationship Coefficients

Sample	Number of two line pedigrees	Inbreeding coefficients		Inter se relationship coefficient
		Actually found	Expected from inter se relationship	
1909	400	5.0 ± .7*	1.9	5.6 ± .8*
1919	400	4.0 ± .6	1.9	5.8 ± .8
1929	400	5.6 ± .6	2.2	4.3 ±1.0
R.O.P.	400	4.4 ± .7	1.1	2.2 ± .7
Show	366	4.7 ± .8	2.8	7.6 ± .7

*Standard Errors

Table III. Comparable sizes of an isolated population breeding at random which would give the observed results

Sample	"Effective number" of males per family or sub-group	"Effective number" of males in entire sample
1909	10	39
1919	17	46
1929	24	41
R.O.P.	17	68
Show	19	23

Table IV. Average number of generations and years to foundation animals

Sample	Average Foundation Year	Generation Interval (yrs.)	Number of Generations
1909	1881	5.8	5.0
1919	1885	5.6	6.4
1929	1894	5.8	6.3
1921*R.O.P.	1892	5.2	7.0
1925*Show	1898	5.2	6.0

*Average birth dates of sample animals

demonstrated with statistical significance unless it were extreme. Also some prominent importations arrived as recently as 1906 and those latest importations could hardly have been blended with the earlier stock by 1909. That is, the history of the importations makes it likely that the breed of 1909 was a mixture of groups, some of which by that date were only beginning to be inter-crossed with each other. By 1919 and still more by 1929 the process of interbreeding those groups might have become nearly complete. The decrease in average inbreeding from 1909 to 1919 and 1929, although not statistically significant, seems logical in view of this breed history.

The amount of inbreeding found is about the same as in other breeds of livestock, especially when considered as the average amount per generation. Our expectation that the unusually small number of foundation animals would lead to an unusually high amount of inbreeding was not fulfilled. Apparently the usual situation that something like one-third to one-half of one per cent of the remaining heterozygosis is lost per generation in pure breeding does not depend so much upon the size or circumstances of the initial population as it does upon breeding customs, such as advertising or other arts of salesmanship which at any one time keep only a few sires or herds in the limelight and cause the great majority of owners to seek sons or grandsons of the few currently famous sires to head their herds. For the inbreeding to be extremely high, either one animal must dominate the situation (as Favourite did the early history of the Shorthorn breed) or many generations must elapse.

Inter se Relationship Coefficient

Some inbreeding would result just because the foundation stock was of limited size and therefore after a few generations any two animals of the breed which might be mated together would inevitably have some ancestors in common, i. e., all mates would be related to each other at least slightly. It might be thought that this would be enough to account for all of the inbreeding observed. This amounts to supposing that at any one date the mating actually was at random with respect to relationship then existing between mates but that the whole breed was closely enough related to give the observed inbreeding coefficients (which are relative to the heterozygosis which existed in the foundation stock).

This was tested by finding the average *inter se* relationship coefficient for each sample and computing from that the inbreeding which would have been found if mating had in fact been random with respect to relationship of mates. (The formula is approximately $F = \frac{R}{2-R}$.)

Table II shows the observed *inter se* relationships and the inbreeding coefficients computed from them. In all five samples the observed inbreeding exceeds the expected and in three of them (the 1909, 1919 and R. O. P. samples) the difference is more than three times its standard error.

It seems clear that there is a little more inbreeding than is made necessary by the general average relationship of members of the breed to each other but it is not clear whether this results from a general tendency of breeders to favor very mild inbreeding over extreme outbreeding or is an average result of a very few breeders deliberately practicing fairly close inbreeding while the great majority practice outbreeding, or is merely a result of the geographical fact that most breeders find it convenient to purchase their sires from nearby herds. Perhaps there are other possibilities?

The Show group is significantly more homogeneous than the other groups, which agrees with the observation that certain of the more recent ancestors show high relationships to the Show sample but only low relationships to the R. O. P. or breed samples. Presumably the small group of breeders who exhibit at the major fairs become well

acquainted with each other's stock and buy from each other more frequently than the average breeders do. Also an animal can become famous as a show winner or parent of show winners at an earlier age than as a high producer or parent of high producers. There would thus be more opportunity while it was still living to spread its blood through the breed or at least through those herds in which it was desired. This difference between the Show sample and the R. O. P. sample is in the same direction as that found in the Holstein-Friesian breed[3] but is more extreme in this case. Neither the Show sample nor the R. O. P. sample is very distinct from the rest of the breed in its ancestry although the Show sample shows some divergence from the rest of the breed in its more recent ancestors.

Population Groups and Average "Effective Number" of Breeding Animals

From a formula by Wright[5] we can estimate the "effective number" of males in a limited population closed to outside blood and with many more females than males appearing as parents. The fraction of the existing heterozygosis lost per generation is approximately $\frac{1}{8M}$ where M represents the effective number of males. Over a period of 8.3 generations this breed, as represented by the 1929 sample, lost 3.8 per cent of its initial heterozygosity. This would be .53 per cent per generation after allowing for the fact that cattle pedigrees traced only one generation (to the parents) cannot show any inbreeding. This would yield 24 as the "effective number" of males. The same group, using the *inter se* relationship coefficient, gives 41 males as the "effective number" of males. The difference in the two numbers is one way of expressing the slight tendency for the breed to be divided into families or sub-groups. Corresponding figures for all groups are given in Table III.

Average Length of Interval Between Generations

The average interval from birth of parent to birth of offspring is 5.4 years for the five groups. This is longer than has been found in similar studies of other breeds. Occasionally an extremely heavy producer at an old age is found. Two of the world's three cows which were over 12 years old when they made yearly butterfat records of over 1,000 pounds are claimed by the Brown Swiss Breed.

Discussion

The first importation of Brown Swiss cattle came to Massachusetts in 1869 and was sold to farmers in that region. The next two importations came to Connecticut in 1882 and 1883. Some of these and a fourth importation went to New York. Some heifers and a bull of the fourth importation were sent to Illinois. The Barton importations, the last of which came in 1906, brought more of these cattle to Illinois, but in a short time they had spread to breeders in Wisconsin, Minnesota, and other midwest regions. Thus during the breed's early history in the United States small colonies of the cattle were formed in widely separated regions. There was only an occasional exchange of stock between regional groups because of the distance involved. Thus some inbreeding naturally developed.

In 1906 the Brown Swiss cattle breeders agreed with the management of the National Dairy Show to have their cattle judged as a dairy breed. Shortly after this agreement the Register of Production was established and the cow College Bravura 2nd made a new high butterfat record. These new policies of the breed association created more mutual interest among the breeders in the various groups and they exchanged new blood with each other to improve their stock according to the new standards.

Since the introduction of new blood to the United States under the present rules is difficult, the homozygosity of the breed in the United States seems cer-

tain to increase. Inbreeding or linebreeding would hasten the action in the group in which it is practiced, but would also increase heterogeneity between the various groups. Doubtless the number of heritable genes in cattle is large, and improvement by mass selection of the desirable genes will be slow, although steady in so far as each gene has an average "good" or "bad" effect as compared with its allel. As inbreeding tends to produce distinct differences between families, selection could become more accurate if combined with some inbreeding. This would be especially important if certain *combinations* of genes have distinctly desirable effects although their constituent genes in other combinations have neutral or undesirable effects. Some form of mild inbreeding to hasten family formation and facilitate selection, with mild outcrosses only when needed to correct undesirable traits, appears to be a better combination for more rapid progress than depending upon selection alone. To some extent that occurred in the early history of this breed.

Summary

No one animal ever dominated the whole Brown Swiss breed in the United States. The highest relationship coefficients found between individual animals and whole groups were in the Show group where sires had values of 14.9 per cent and 14.2 per cent, and cows were as high as 13.5 per cent and 9.5 per cent. The highest relationship coefficients between single animals and the general breed samples were 9.2 per cent (William Tell in 1909) and 9.1 per cent (College Boy in 1929).

The inbreeding found was equivalent to a loss of about one half of one per cent of the existing heterozygosis per generation, which is much the same as that found in other breeds.

There was a small but significant excess of inbreeding over what would have happened if mating had been truly random with respect to relationship between mates. This indicates some tendency to family formation, which, however, rarely goes far.

The Register of Production group is composed of relatively unrelated animals and does not show any tendency to be a distinct family within the breed.

The Show group is more closely interrelated and shows some slight tendency to be different from the breed average in its relationship to a few recent ancestors.

The early history in the United States indicates high heterogeneity because the groups were rather isolated. This decreased when breeders began to exchange breeding stock over a broader area.

The average interval from the birth of parent to the birth of offspring is 5.4 years.

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